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ALLELOPATHIC EFFECTS OF *LANTANA CAMARA* (VERBENACEAE) ON MORNING GLORY (*IPOMOEA TRICOLOR*)

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ABSTRACT

Allelopathic effects of *Lantana camara* L. foliar leachates and dried leaf amendments on *Ipomoea tricolor* Cav. radicle growth, shoot emergence, and plant biomass were examined over a 50-day period. Aqueous leaf extracts of *L. camara* decreased radicle growth of *Ipomoea* but germination percentage was not inhibited. Dried leaf residue in soil growth media delayed shoot emergence from soil. Plant biomass after 50 days was not affected by the presence of *L. camara* soil amendments. Leaf extracts in petri dishes were more inhibitory than was dried leaf material in soil. These results indicate the presence of phytotoxic compounds in *L. camara.* Allelopathic effects of these compounds are significant during early germination of *Ipomoea,* while plants older than 2 weeks appear unaffected. In the soil environment allelopathic effects are minimal, possibly due to chemical binding, microbial action, or both.

Key Words: allelopathy, exotic weeds, germination, *Ipomoea, Lantana,* morning glory

INTRODUCTION

Lantana camara L. (Verbenaceae) is a shrub of West Indian or South American origin (Schemske, 1983) that is considered one of the world's worst weeds (Holm et al., 1971). It grows in moist open soil and flowers throughout the year. Proliferation in Australia and the United States has been facilitated by its introduction as an ornamental. Along the edges of Australian rainforests in Queensland, *L. camara* thickets persist for decades. I have observed these thickets encroach on native vegetation and restrict rainforest regeneration. In Florida, *L. camara* has been listed as a "Category I" exotic pest by the Florida Exotic Pest Plant Council since 1991. Category I designates those species invading or disrupting native plant communities in Florida. The list places *L. camara* among the state's most invasive plants including *Casuarina, Melaleuca,* and *Pueraria* (Exotic Pest Plant Council, 1992).

Although sensitive to frost, *L. camara* occurs throughout much of Florida (Figure 1), and is reported to be a problem in pastures and in nature preserves (Gregg, 1994). Eradication efforts by mowing, herbicides, and burning cost millions of dollars annually

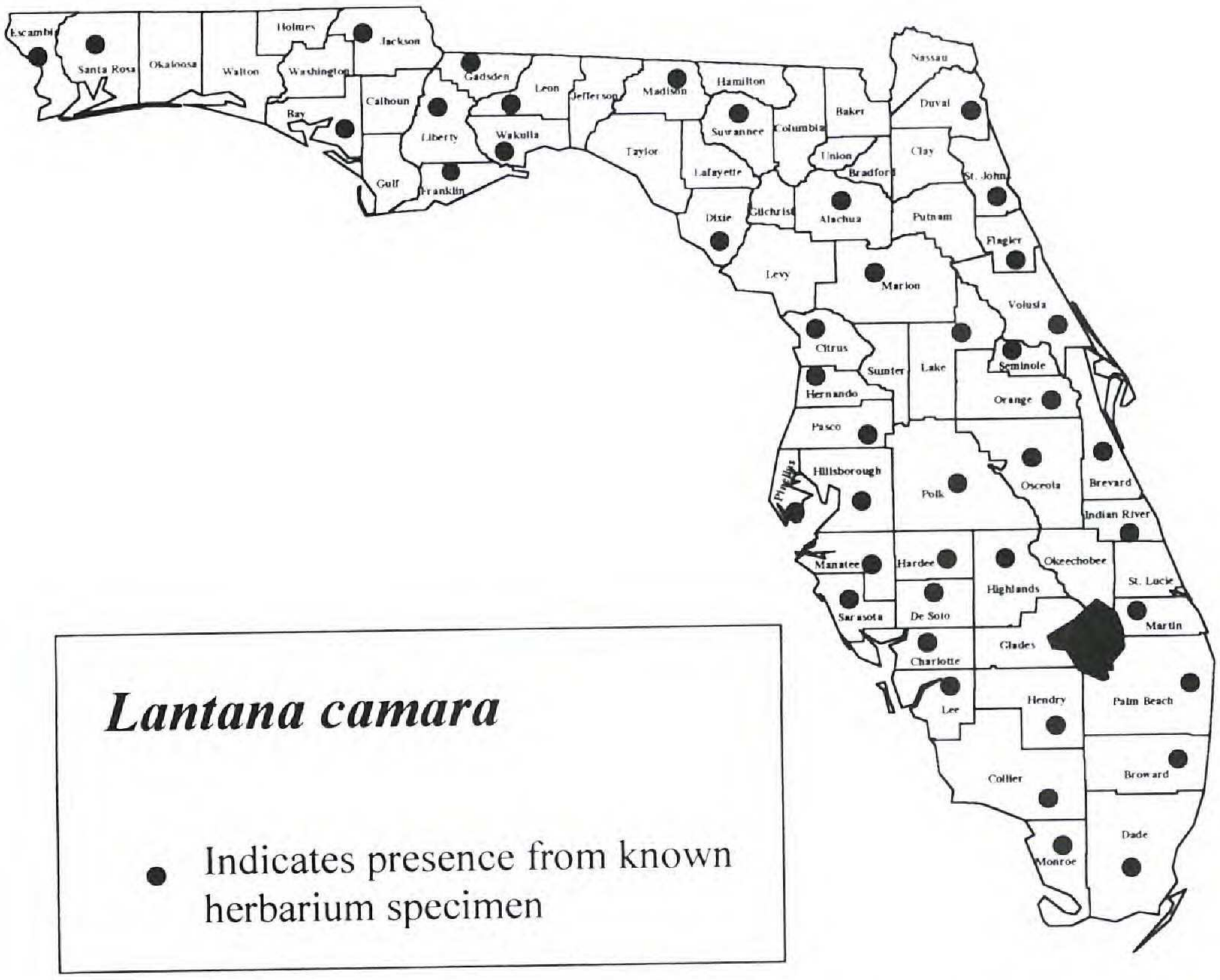

Figure 1. Distribution of *Lantana camara* in Florida counties (adapted from Wunderlin et al., 1995).

(Gregg, 1994). In citrus groves, *L. camara* has been observed to interfere with application of fertilizer, herbicides, and with harvesting (Achhireddy and Singh, 1984). The weed is toxic and potentially lethal to livestock and children (Mortan, 1971). Its tendency to develop pure stands in diverse environments (Achhireddy and Singh, 1984) has led workers to study the basis for the competitive success of *L. camara*.

Allelopathy, as defined by Rice (1984) is a harmful chemical effect by one species upon another. It is more specific than competition because it depends on the addition of a chemical compound to the environment by the inhibitory (allelopathic) species. *Lantana camara* has been shown to be allelopathic to Milkweed Vine (*Morrenia odorata*) in soil assays (Achhireddy and Singh, 1984) and to Duckweed (*Lemna spp.*) and Ryegrass (*Lolium*) in the laboratory (Jain et al., 1989; Singh et al., 1989). Thirteen allelopathic compounds have been identified in leaves of *L. camara* (Jain et al., 1989).

In this study on the extent of allelopathic effects of *L. camara,* I used Heavenly Blue morning glory (*Ipomoea tricolor* Cav.) as the test species. Genetically uniform seed lots of this cultivar are commercially available, and it is closely related to *I. purpurea* (L.) Roth. naturalized (introduced but non-intrusive) throughout Florida and much of the eastern seaboard of the United States. In Florida, *Ipomoea* occurs with *L. camara* in cypress-pine re-growth forests and in similar subclimax forest communities. However, it has not been observed using *L. camara* as a support, suggesting that *L. camara* might be inhibiting the growth of *Ipomoea* nearby. In this study, the presence of compounds in *L. camara* which might be allelopathic against *Ipomoea* was tested by germinating *Ipomoea* seeds in aqueous extracts of *L. camara,* and by growing seedlings of *Ipomoea* in potting soil to which dried leaves of *Lantana* had been added. A reduction of *Ipomoea* growth in *Lantana*-laced media (vs. the same media but without *Lantana* extract or dried leaves) would support the idea that allelochemicals are at least partly responsible for the ability of *Lantana* to grow as pure stands, free of *Ipomoea* and other naturalized and native species in Florida.

MATERIALS AND METHODS

Petri Dish Assays

Shoots of *L. camara* were collected in January 1994 from a disturbed site on 107 Ave, Homestead, Florida. Leaves were then air dried at 80°C. A 5% aqueous extract was made by steeping 5 g of *L. camara* leaves in 100 ml deionized water at 25°C overnight, then filtering the solution through Whatman No. 1 paper. The extract (designated as 5%) was diluted with deionized water to make 2.5% and 1.25% solutions using methods similar to those of Achhireddy and Singh (1989). The pH of all extracts ranged between 6.7 and 7.0.

Seeds of *Ipomoea tricolor* (Heavenly Blue morning glory) were purchased from Johnny's Selected Seeds in Albion, Maine, and rinsed overnight in running tap water. Those which had swollen and showed emerging radicles were then used in petri dish assays and in soil assays (below). Ten swollen seeds were placed in each petri dish. Dishes contained filter paper wetted with 10 ml of aqueous *L. camara* leaf extract at 5%, 2.5%, 1.25%, or 0% (water

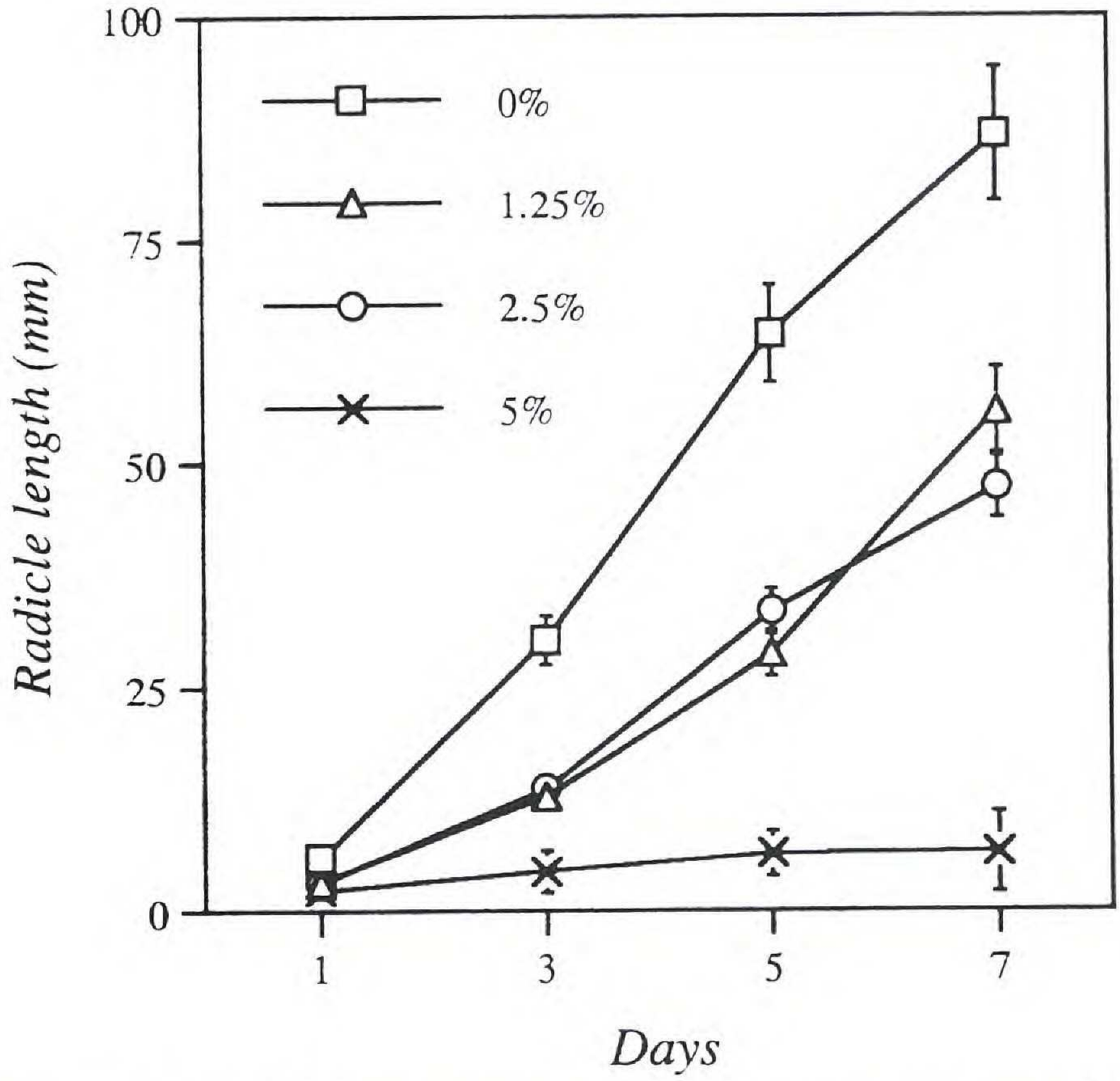

Figure 2. Length of *Ipomoea* radicles on seeds sprouting in aqueous *Lantana* extract (0–5%) over the course of one week. Each point represents the average of 30 radicles. In these petri dish assays, radicle growth was slowest in seeds soaked in the highest concentration (5%) of *Lantana* extract. Bars show ±1 SE; bars are absent when ±1 SE ≤ height of symbol.

control). They were kept at 25 ± 2°C under a 12h–12h light–dark cycle. Three replicate assays were performed, requiring a total of three petri dishes and thirty seeds for each of the four leaf extract preparations. Germination rate and percentages by seeds imbibing *Lantana* extract were examined using the methods of Liebl and Worsham (1983). Germination (root emergence), and radicle length were monitored over the course of seven days. Radicle lengths of seedlings in each concentration of *Lantana* extract were averaged (Figure 2).

Soil Assays

To expose *Ipomoea* seedlings to *Lantana* residue within a soil environment, five concentrations of leaf-amended soil were made. Each contained 300 g of sterilized commercial potting soil, then

12 g, 6 g, 3 g, 1.5 g, or 0 g (control) of dried and crushed *L. camara* leaves. Crushed leaf material was thoroughly mixed into the potting soil. The soils, now containing *Lantana* leaf residue, were watered and allowed to drain overnight before being planted with *Ipomoea* seeds. In each soil preparation, ten seeds (soaked in tap water, as above) were planted 2 cm deep and 2 cm apart. Three replicate assays were performed, requiring a total of three pots and thirty seeds for each amended soil preparation. Pots were kept in a greenhouse under 14h days with diurnal temperatures fluctuating between 10–30°C. Shoot emergence rate was monitored over 14 days (Figure 3). Seedlings were left to grow in the greenhouse, and total fresh biomass of root and of shoot systems was measured after seven weeks (Figure 4).

Analysis of variance (ANOVA) was used to test for significant differences between means, with a Scheffé posthoc multiple comparison test to determine whether means of the dependent variable differed significantly at P levels from 0.05 to 0.0001 (Data Desk 4.0, Data Description Inc. Ithaca, NY).

RESULTS

Petri Dish Assays

When exposed to *L. camara* extract, seeds of *Ipomoea* germinated at a rate similar to that of seeds in deionized water. Within 48 h of being placed on wetted filter paper, 90–100% of seeds germinated regardless of the concentration of *L. camara* extract used to wet the filter paper. After seven days, seedlings in all treatments showed distinct radicles. However, seedlings growing on paper soaked with 5% *L. camara* extract suffered up to 50% mortality apparently due to microbial activity fostered by nutrients in the extract. Seed putrifaction was common in 5% extract, but was never found in seeds soaked in water as a control. Only healthy seedlings with turgid white radicles were used in measuring radicle length. Thirty uncontaminated seedlings were measured from each treatment.

Once germinated, *Ipomoea* seedlings exposed to high concentrations of *L. camara* extract developed significantly ($P \leq 0.001$) shorter radicles than did control seedlings in deionized water (Figure 2). Though significant ($P \leq 0.01$) radicle inhibition occurred in seedlings growing in *L. camara* extract at 1.25% and at

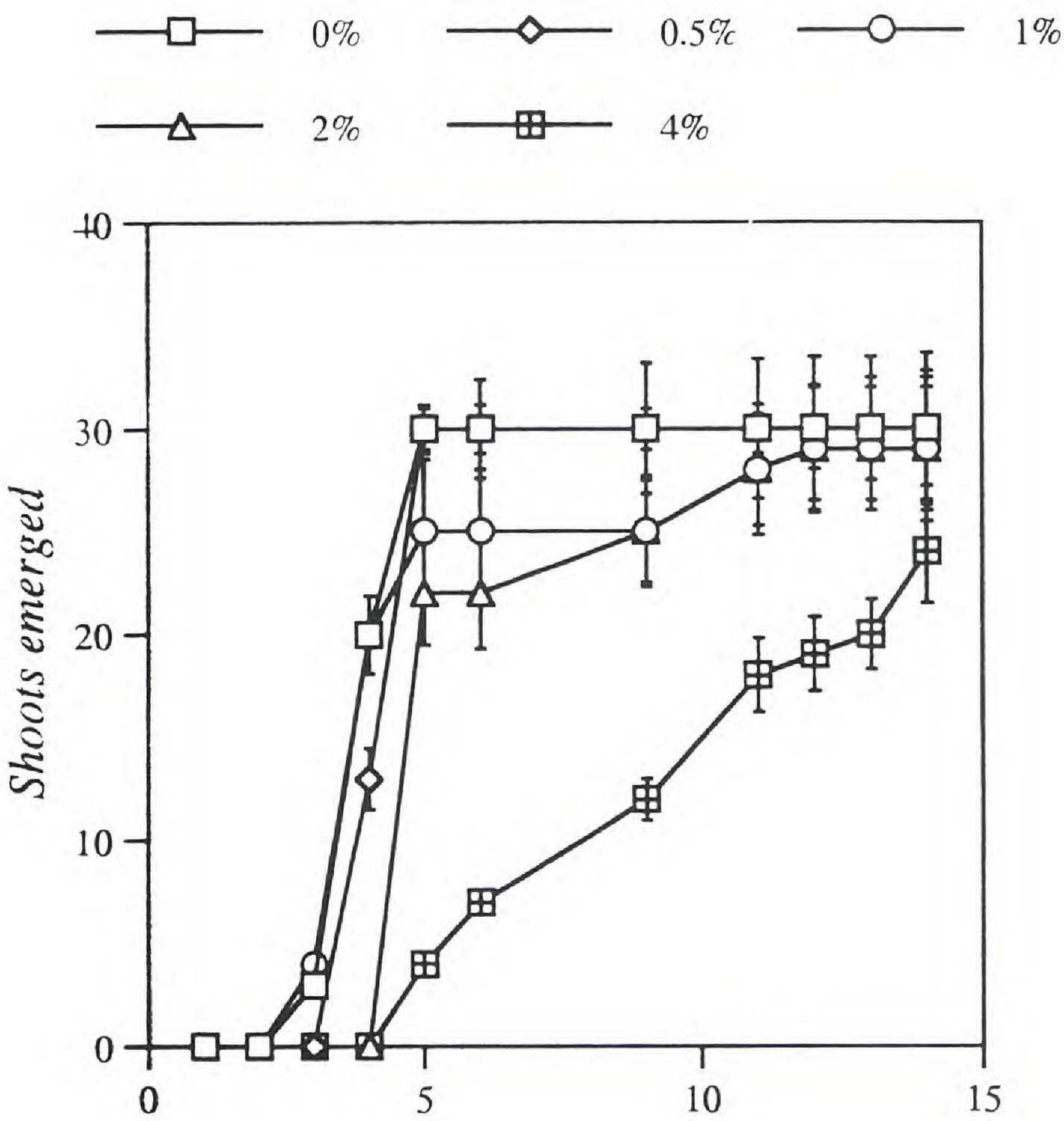

Figure 3. Rate of *Ipomoea* seedling emergence from soils laced with dried *Lantana* leaf material (0–4% by weight). Thirty seeds were planted in each of the five concentrations of *Lantana*-laced soil. Each point represents the average of 30 seedlings. A significant delay in seedling emergence occurred in *Ipomoea* growing in soil amended with 4% *Lantana* leaf material. Bars show ±1 SE; bars are absent when ±1 SE ≤ height of symbol.

2.5%, the most pronounced inhibition of seedling growth was caused by 5% extract. In that solution, radicles seldom reached more than a centimeter, while over the same amount of time, radicles of control seedlings in deionized water grew to ten times that length.

Soil Assays

The rate of *Ipomoea* shoot emergence from soil was slowed in the presence of *Lantana* leaf material (Figure 3). The most rapid

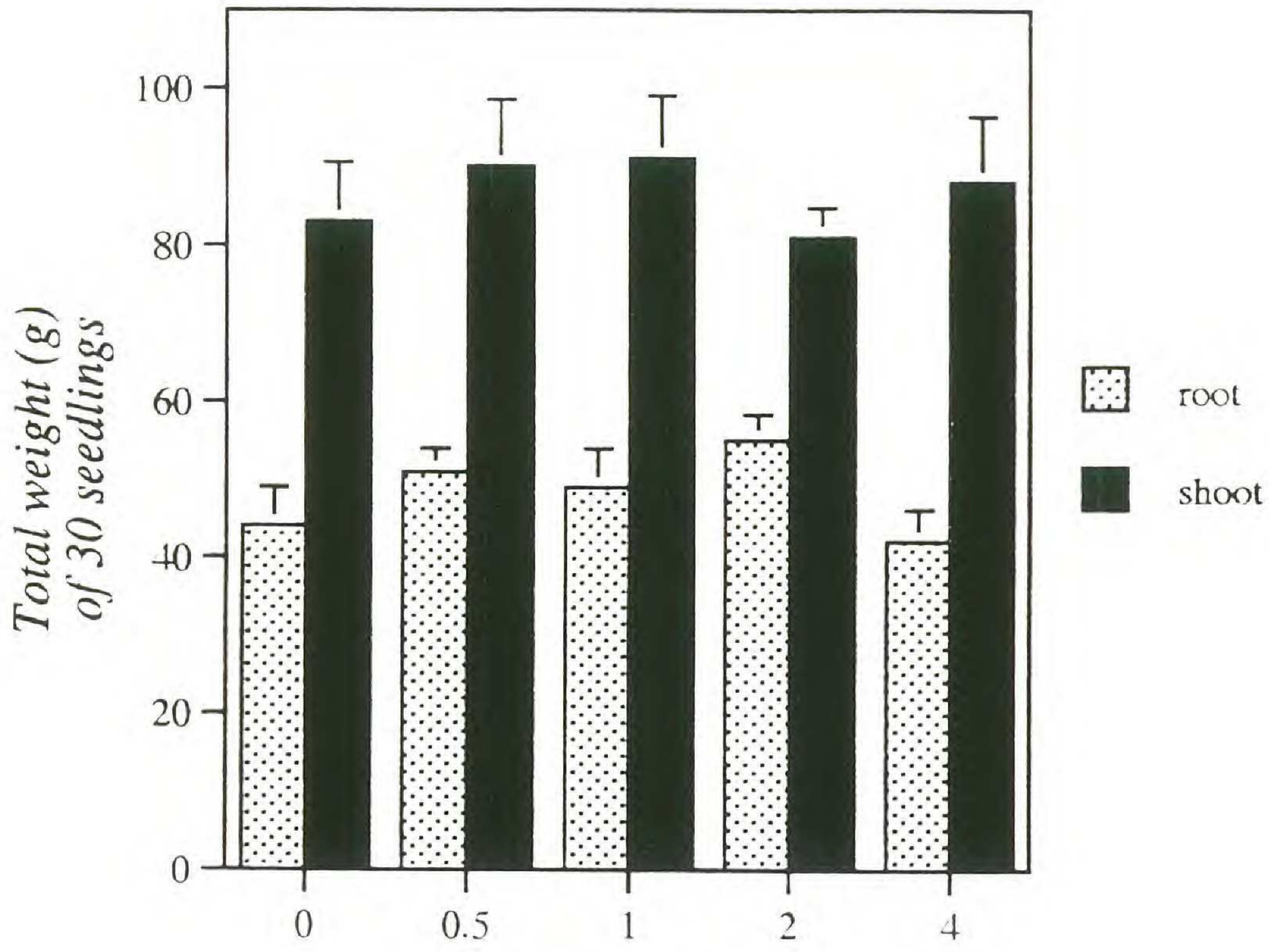

Figure 4. Total root and shoot biomass (fresh weight) of *Ipomoea* plants grown 50 days in soil laced with dried *Lantana* leaf material (0–4% by weight). Each bar represents the total fresh weight of roots or shoots from 30 plants. Error bars are +1 SE.

emergence was seen in control pots containing only potting soil, not amended with *Lantana*. In more than 90% of cases, cotyledons emerged from control soil within 4–5 days of being planted. In soil amended with dried *Lantana* leaves the rate of seedling emergence slowed with increasing concentrations of leaf material. Compared to control sets which had completely emerged after 4–5 days, seedlings in soil laced with 4% leaf material required significantly longer time ($P \leq 0.01$) to emerge, typically twice as long as did controls. Regardless of the time required for cotyledons to emerge, the appearance and subsequent development (leaf morphology, internode length, tendril activity) of *Ipomoea* seedlings was similar in amended and in control soils.

Two months after growing in the greenhouse, all 150 *Ipomoea* plants (10 plants for each of 5 *Lantana* leaf amendments to soil; 3 replicates) were removed from their pots, washed clean of soil

particles, dabbed clear of water droplets and divided into root and shoot components. Total fresh weights of shoots and roots from three sets of plants (10/set) growing in each concentration of *L. camara* leaf amendment were determined (Figure 4). Within any given pot containing a set of ten plants, there was variation in plant size. Shoot systems weighed nearly twice as much as did root systems, and plants with smaller shoots had smaller root systems. There was no significant ($P \leq 0.05$) variation in shoot and root total fresh weight among sets of plants grown in the same or in different concentrations of *L. camara* leaf amendment. Plants in heavily contaminated soil (amended with 4% *L. camara* leaf material) grew as well as did control plants in uncontaminated soil. There was even a qualitative improvement in plants growing in soil laced with *L. camara*. After two months of growth, *Ipomoea* plants in soil containing 0% and 0.5% *Lantana* leaf material were yellowing, while those growing in heavily laced (4%) soil were still green.

DISCUSSION

The potentially allelopathic effect of *L. camara* against *I. tricolor* is expressed as a delay in early (underground) seedling growth, while post-emergence seedling and plant growth seem unaffected. In this study, I found growth of *I. tricolor* to be inhibited (delayed and reduced) by *L. camara* leaves, primarily when *Ipomoea* seeds were forced to imbibe aqueous extracts of *L. camara* in a petri dish (Figure 2). The effect of *Lantana* residue in soil appears to be less severe. After an initial delay in seedling emergence (Figure 3), *Ipomoea* plants growing in *Lantana*-laced soil show no ill effects, even after 50 days of growth (Figure 4). In fact, the greener appearance of plants in heavily laced soil is probably due to increased nutrients supplied by decaying *Lantana* leaf material, while plants growing in unamended potting soil develop nutrient deficiency symptoms such as chlorosis.

Results of this study differ from those reported by Achhireddy and Singh (1984). They used similar methodology to amend soil with dried leaves of *L. camara* and found that biomass of another vine, *Morrenia odorata* (Asclepiadaceae), was reduced by 33% when plants were grown in soil containing 4% *Lantana* leaf material. Growth inhibition was apparent after 30 days, whereas in

the present study using *Ipomoea,* no biomass difference between control plants and those growing in *Lantana* laced soil appeared even after 50 days (Figure 4). Recent work by Inderjit and Dakshini (1994) suggests that leaf amendments in soils can change soil texture, and that test plants growing in amended soils could respond to textural as well as chemical changes caused by leaf amendments. The most significant inhibitory effects of *Lantana* material upon *Ipomoea* take place in the earliest phase of seedling growth. Radicle growth is delayed in germinating seeds confined to petri dishes (Figure 2) as is initial shoot emergence from soil (Figure 3). Under field conditions, delayed early growth can be fatal. Slow-growing seedlings are vulnerable to soil pathogens and herbivores, and require more time for roots to penetrate to soil levels with reliable moisture, several inches beneath the hot surface.

In situations where seeds are exposed to *Lantana* leachate in a confined environment, such as a petri dish, any inhibitory (allelopathic) compounds present in the growth medium will affect seedling growth. On the other hand, in open systems such as potted soil or disturbed sites populated by *Lantana* and *Ipomoea* in the field, potentially allelopathic material in *L. camara* may bind to organic molecules such as humic acid (Wang et al., 1971), soil colloids, or be broken down by bacteria or physical processes. This would decrease their potential to inhibit growth in the field (Rice, 1984). In a study of allelochemicals binding to organic matter in two Taiwanese agricultural soils (Wang et al., 1971) five phenolic acids, all of which are present in *L. camara* (Singh et al., 1989), were added to field soil. Between 60% to 80% of all added phenolics were bound to mudstone and latosol components of the soil. Ferulic acid, a phenolic in *L. camara* with strong inhibitory activity (Jain et al., 1989), was strongly bound by the soils, with the result that only 2–30% of applied ferulic acid remained free.

For *L. camara* to be functionally allelopathic against *Ipomoea* in the field, it must release inhibitors that are not inactivated by soil components. Strong inhibition occurs in petri dish assays (Figure 2) but *Lantana* material has less effect when delivered to seedlings in a soil medium. Inhibition is reduced (Figure 3) and dwindles to insignificant levels over the course of 50 days (Figure 4). It might still be possible for *Lantana* to allelopathically inhibit *Ipomoea* and other plants in the field but it would require constant

replenishment of allelopathic compounds to soil through leaf drop or root exudates.

Given the remarkable success of *L. camara* as a pantropical weed and its wide distribution in Florida (Figure 1), the competitive strategies of this pest are worth exploring. Possible mechanisms leading to pure stands of *Lantana* include spatial and nutrient competition, coupled with the slight advantage of delay in germination of competing seedlings, as shown in this study with *Ipomoea*. Given the magnitude of damage and management costs caused by exotic pest plants (Gregg, 1994), understanding the means by which exotic weeds such as *L. camara* dominate local vegetation is needed to develop efficient and environmentally benign methods of exotic weed control (Heisey, 1996). That in turn will help sustain native flora in preserves, along with areas that have been repaired or restored (Kaufman and Franz, 1993).

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